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Circumfacial Markings in Siamang and Evolution of the Face Ring in the Hylobatidae

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The occurrence of a white brow band in siamang is documented for the first time. The characteristic occurs in 4.4% of 250 siamang. Among adult siamang the characteristic occurs more often in females than in males (11.3% of 71 females vs. 1.4% of 73 males). In a particular family lineage of captive siamang (not included in the numbers above), the characteristic was unusually frequent (42.9% of 14). The trait appears to be inherited, possibly as an autosomal dominant inheritance. Additional white markings occur in at least one of the subjects on hands, feet, and in a corona above the ears. In contrast to other studies, our results suggest that the presence of white facial markings, and possibly also of white hands and feet and of a bright corona are primitive gibbon traits. In addition, some degree of sexual dichromatism in the circumfacial markings appears to have occurred in the common ancestor of all gibbons.

KEY WORDS: *Symphalangus syndactylus*; siamang; gibbon; face ring; fur coloration; evolution.

INTRODUCTION

One of the most conspicuous and well-known characteristics of the fur coloration of many gibbons (Hylobatidae) is the white, or at least bright, circumfacial pattern (Geissmann, 1994, 1995). In some species, the pattern consists of a closed band bordering the whole contour of the dark and almost

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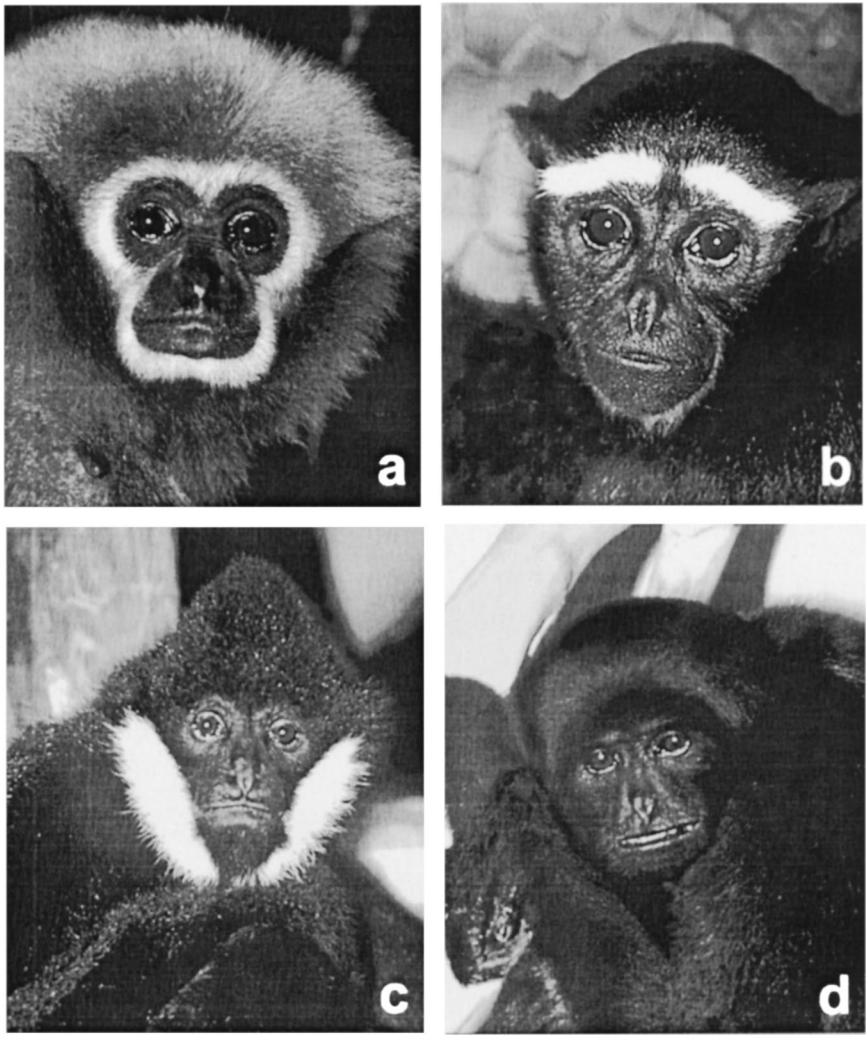

Fig. 1. Circumfacial patterns in gibbons: (a) *Hylobates lar*, adult female; (b) *Bunopithecus hoolock*, juvenile male; (c) *Nomascus leucogenys*, adult male; (d) *Hylobates klossii*, adult male.

naked facial area. It is then usually called a face ring (Fig. 1a). In other species, the circumfacial pattern may be reduced to a brow band (Fig. 1b), and in yet other species the pattern may be reduced to the cheek region (Fig. 1c). In black crested gibbons (*Nomascus concolor* and *N*. sp. cf. *nasutus*), the

circumfacial pattern is absent in adult males, but traces of it sometimes occur in adult females. In two species, the facial pattern is completely absent in both sexes: in Kloss gibbons (*Hylobates klossii*) and in siamang (*Symphalangus syndactylus*) (Fig. 1d).

Groves (1972) mentioned having seen a captive siamang with a face ring, and other siamang with traces of face rings. Unfortunately, he did not document this in more detail, and it is difficult to decide how far his observations can be compared with the facial markings of other gibbons. In contrast to Groves, Haimoff *et al.*. (1982, p. 222) stated:

> "Male siamang and Kloss gibbons have no face markings, and although Groves [1972] mentions some siamang specimens with a very faint face ring, this phenomenon is rare and equated with old age [Chivers, personal observation; Haimoff, personal observation]. . . . The females are generally the same . . ."

In the dark face of siamang, some short white hairs are usually present, especially in the lower half of the face. They may become gradually more dense toward the periphery of the face. I have observed this facial hair in >100 captive siamang of various ages. It can also occur in other gibbons. It is unclear whether the white facial hairs are in any way related to the face ring pattern of other gibbon species. It is possible that one or both of the two studies mentioned above were actually referring to such facial hair when discussing the occurrence of face ring markings in siamang.

I report, the occurrence of a white brow band in siamang for the first time. The brow band differs from the faint face ring in old siamang (Haimoff *et al.*, 1982). In addition, I demonstrate that the brow band is probably related to the face ring pattern of other gibbon species. I estimate the frequency of the brow band for adult and immature, and male and female siaman, and discuss the ontogenetic aspects of the characteristic. In addition, I describe the genealogy of the brow band pattern in a large family lineage of captive siamang.

MATERIAL AND METHODS

The gibbon classification used here follows Geissmann *et al.* (2000).

I collected data on the distribution and frequency of the brow band pattern in siamang from 1980 to 2001 in zoos and museum collections.

I observed captive siamang in China (Hong Kong); France (Doué la Fontaine); Germany (Berlin Zoo; Dortmund; Duisburg; Frankfurt; Zoo Hellabrunn, München); Indonesia (Ragunan Zoo, Jakarta; Taman Safari, Cisarua); Portugal (Lourosa); Switzerland (Zoo "Seeteufel," Studen;

Zürich); the United Kingdom (Banham; Howletts; Twycross); and the U.S.A. (Metro Zoo, Miami).

Zoo siamang >6 years are adult Geissmann (1991), and all younger animals are immature siamang. In the statistical analysis, I assigned zoo subjects monitored over several years to the age class they had when I last saw them. Neonatal siamang which had not yet developed a black fur coat are not in the study.

Many siamang with white brow bands were members of an extended family originally living at the Duisburg Zoo in Germany. I visited them several times during the study and also included several family members that had been transferred to other zoos. I took photographs and made drawings of most of the Duisburg siamang during two visits on 23–26 June 1987 and on 2–3 March 1988. Additional photographs and descriptions of animals born subsequently were kindly made available by Dr. M. Orgeldinger, Mr. J. Hammes and Ms. B. Minnemann.

I examined siamang skins in Austria (Naturhistorisches Museum, Wien, NHMW), France (Muséum National d'Histoire Naturelle, Paris, MNHN), Indonesia (Museum Zoologicum Bogoriense, Bogor, MZB), the Netherlands (National Museum of Natural History, Leiden, MRNH), Germany (Zoologisches Museum der Humboldt-Universität Berlin, ZMB; Staatliches Naturhistorisches Museum, Braunschweig, SNHMB; Staatliches Museum für Tierkunde, Dresden, SMTD; Natur-Museum Senckenberg, Frankfurt, NMS), Sweden (Naturhistoriska Riksmuseet, Stockholm, NHRM), Switzerland (Naturhistorisches Museum Basel NHMBa; Naturhistorisches Museum Bern NHMBe; Anthropologisches Institut und Museum der Universität Zürich, AIMUZ; Zoologisches Museum der Universität Zürich, ZMZ), the United Kingdom (British Museum (Natural History), London, BM(NH)), and the U.S.A. (American Museum of Natural History, New York, AMNH; Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, MCZ; National Museum of Natural History, Washington, D.C., USNM).

I identified adulthood of museum specimens based on dental eruption, dental wear and the fusion of the basicranial suture, i.e. the speno-occipital synchondrosis, and, if no skull was available, on the overall size of the skin and—in females—the size of nipples.

Unless noted otherwise, I took all photographs.

I adapted non-parametric statistical tests (Fisher exact [probability] test and Chi-square test) from Siegel and Castellan (1988). All tests are two-tailed, with a significance level of 0.05.

Because the Duisburg siamang may exhibit a highly atypical concentration of the brow band, I conducted all statistical calculations both with and without them.

RESULTS

Frequency and Distribution of the Brow Band Pattern

I systematically checked a total of 264 siamang for the presence or absence of the brow band (Table I). They include 145 museum skins and 119 captives (105 if the Duisburg colony is excluded). There is a total of 17 brow-banded siamang, 6 of which were members of the Duisburg linege. (Appendix).

The brow band exhibits some variability. In adult siamang, it consists of a whitish, light gray or light yellow band above the eyes, clearly outside but adjacent to the facial area. The brow band often is slightly narrower in the middle part, but not separated, and it is thicker at the lateral ends. In this case, it is quite similar to the facial markings in male hoolock gibbons or in female agile gibbons (*cf.* Figs. 1b and 3). Brow bands that are thickest centrally appear to be less common. The thickness also varies from a very narrow stripe to a broad band which may be >1.2 cm thick. Two individuals also exhibited some short pale hairs above the ears and on the toes. A Duisburg female, Trine (Fig. 4a) has a distinct tuft of long white hair above each ear. In addition, her halluces are covered with pure white fur (Fig. 4b). The dorsal surfaces of the middle phalanges of her hands and feet also are covered with white hair, but they are intermixed with dark hair, especially on the hands. Her distal phalanges are bare.

If the Duisburg siamang are included in calculations, the overall frequency of the brow band phenotype in all sample siamang is 6.4% (17 of 264). The brow band occurs in 2.8% (4 of 145) of museum specimens, but in 10.9% (13 out of 119) of zoo specimens. The difference is statistically significant (Chi-square test, $p < 0.008$).

The Duisburg lineage probably includes an atypical concentration of siamang with the brow band pattern. If the calculations are repeated excluding the Duisburg siamang, the overall frequency of the brow band phenotype is reduced to 4.4% (11 of 250), and it occurs in 6.7% (7 of 105) zoo specimens. If the Duisburg lineage is excluded, the difference between zoo and museum specimens is not statistically significant (Chi-square test, $p > 0.5$).

Six of 14 siamang (42.9%) in the Duisburg lineage exhibit the brow band. It is much higher than in the remaining zoo sample (7 of 105). The difference is highly significant (Fisher exact text, $p = 0.0009$) and supports the view that the Duisburg lineage is a very atypical sample.

In the combined zoo and museum sample of adult siamang with known sex ($n = 144$, excluding the Duisburg siamang), the brow band occurs more frequently in females (11.3%, 8 of 71) than in males (1.4%, 1 of 73). It may even be questioned whether the one brow banded male in the sample

Table I. Absolute number and percentage of siamang with light brow band patterns in museum collections and zoos, excluding the Duisburg siamang lineage[a]

	Museum siamangs			Zoo siamangs			Total siamangs		
	All	Brow Band		All	Brow Band		All	Brow Band	
Age class and sex	n	n	%	n	n	%	n	n	%
Adult males	44	0	0.0%	29 (32)	1 (1)	3.4% (3.1%)	73 (76)	1 (1)	1.4% (1.3%)
Adult females	43	4	9.3%	28 (32)	4 (8)	14.3% (25.0%)	71 (75)	8 (12)	11.3% (16.0%)
Adult unsexed	18	0	0.0%	0	0	0.0%	18	0	0.0%
Immature males	13	0	0.0%	32 (39)	1 (3)	3.1% (7.7%)	45 (52)	1 (3)	2.2% (5.8%)
Immature females	18	0	0.0%	13	1	7.7%	31	1	3.2%
Immature unsexed	9	0	0.0%	3	0	0.0%	12	0	0.0%
Total siamangs	145	4	2.8%	105 (119)	7 (13)	6.7% (10.9%)	250 (264)	11 (17)	4.4% (6.4%)

[a]The numbers resulting from inclusion of the Duisburg individuals are in parentheses.

actually exhibits a brow band or an unrelated characteristic, because his light hairs are not directly above his eyes, but instead higher up on the forehead (Appendix). The sex difference in the frequency of the brow band is statistically significant (Fisher exact test, $p = 0.0167$). If the arguably brow banded male is excluded from the sample, the frequency of the brow band in adult males drops to 0% ($n = 72$) and the sex difference is even more significant (Fisher exact test, $p = 0.003$). If the male is retained but the Duisburg lineage is included in the sample ($n = 151$), the proportion of adult females with a brow band rises to 14.7% and the significance is also more pronounced (Fisher exact test, $p = 0.0011$).

The Duisburg Genealogy

The Duisburg lineage comprises 4 generations (Fig. 2).

Five of the 14 siamang from Duisburg sport the brow band (Fig. 3). Hexe probably grew up at the Duisburg Zoo together with another siamang, Piet which does not show the characteristic. The hand-reared individuals comprise one individual with and 2 without a brow band, Which makes it likely that the characteristic in siamang is controlled by genetic factors rather than by other factors such as environmental influences.

The pedigree (Fig. 2) revealed that all individuals with the brow band are related to each other. Unfortunately, the mode of inheritance cannot be reliably determined from the small pedigree. If the inheritance were recessive, all breeding females must be homozygous for the characteristic, because they all show the white brow band. Likewise all breeding males must be heterozygous, because they all have no brow band but produce offspring with the brow band characteristic. In view of the rarity of the characteristic, such an accumulation of homozygous individuals seems to be relatively unlikely. Dominant inheritance appears to be more probable. Here, all breeding males must be homozygous non-carriers of the hypothetical brow band allele, because none exhibits the characteristic. The first breeding female, Hexe, could either be homozygous or heterozygous for the characteristic (one allele is enough for phenotypic expression), but her daughters are heterozygous, because they can only inherit one allele for the characteristic from their mother.

Ontogeny

Figure 4 shows one of the 3 Duisburg females, Trine, at 8 mo and documents the presence of the brow band in the infant, which clearly shows that the characteristic is not a phenomenon restricted to old siamang, as with the face pattern described by Haimoff *et al.* (1982).

The brow band in adult siamang consists of an uninterrupted area of light fur. In contrast, the brow band consists of separated patches above the

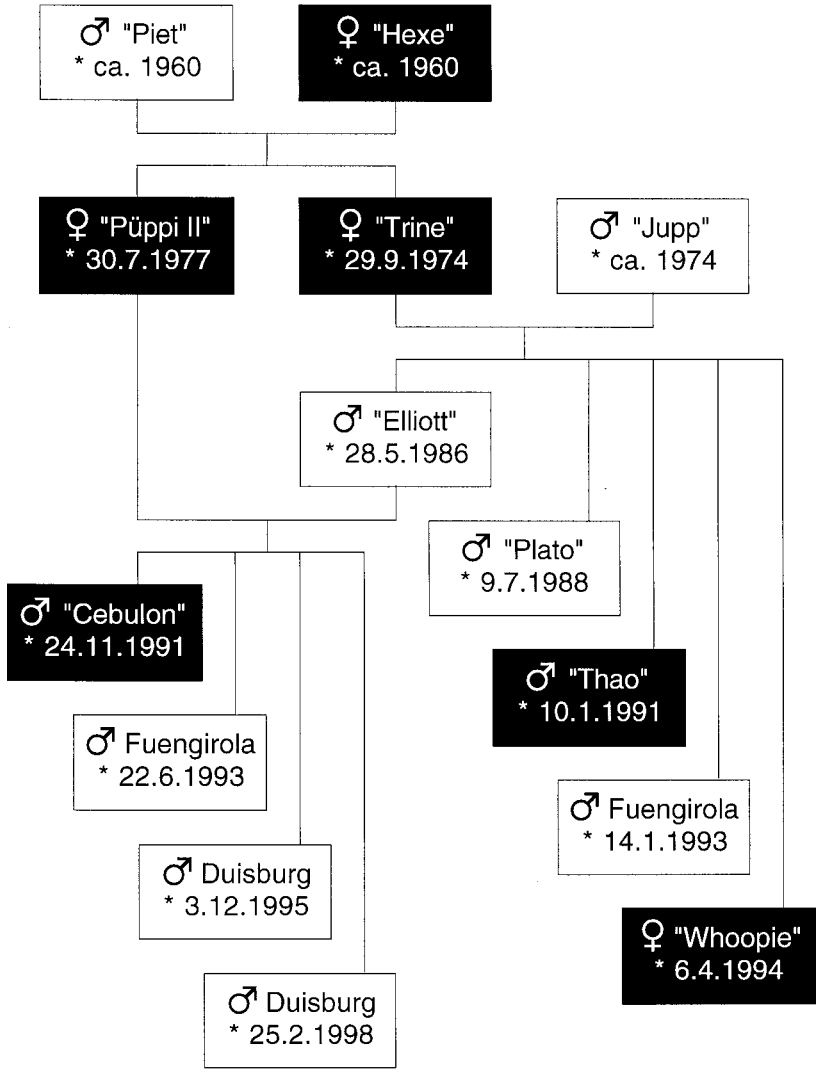

Fig. 2. lineage and birth dates of the siamang at the Duisburg Zoo. Black rectangles indicate individuals with a brow band.

eyes in immature siamang. Apparently, the patches grow medially during ontogeny until they connect over glabella though the connection is very thin in some siamang.

One male, Thao, born at Duisburg Zoo, did not have a distinct brow band when 6 mo old, as documented by photographs kindly provided by Mr. M. Orgeldinger. However, the pattern started to develop when he was about

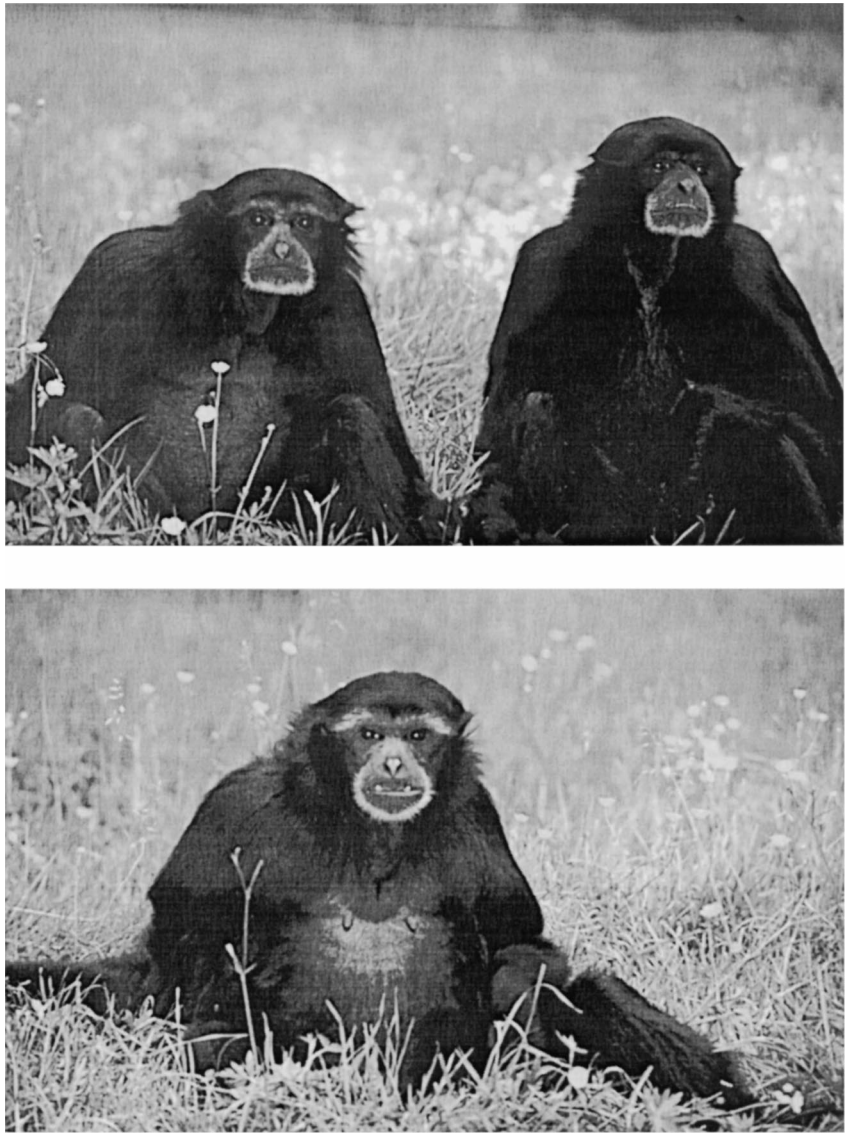

Fig. 3. Siamang at the Duisburg Zoo (21. June 1987). Above: Adult female (Püppi II, left) and adult male siamang (Piet, right). Note the conspicuous white brow band in the female, and the absence of the characteristic in her father. Below: Adult female siamang Hexe at the Duisburg Zoo. The distinct white brow band of this female is slightly broader at the lateral ends than the brow band of her daughter in the upper photograph.

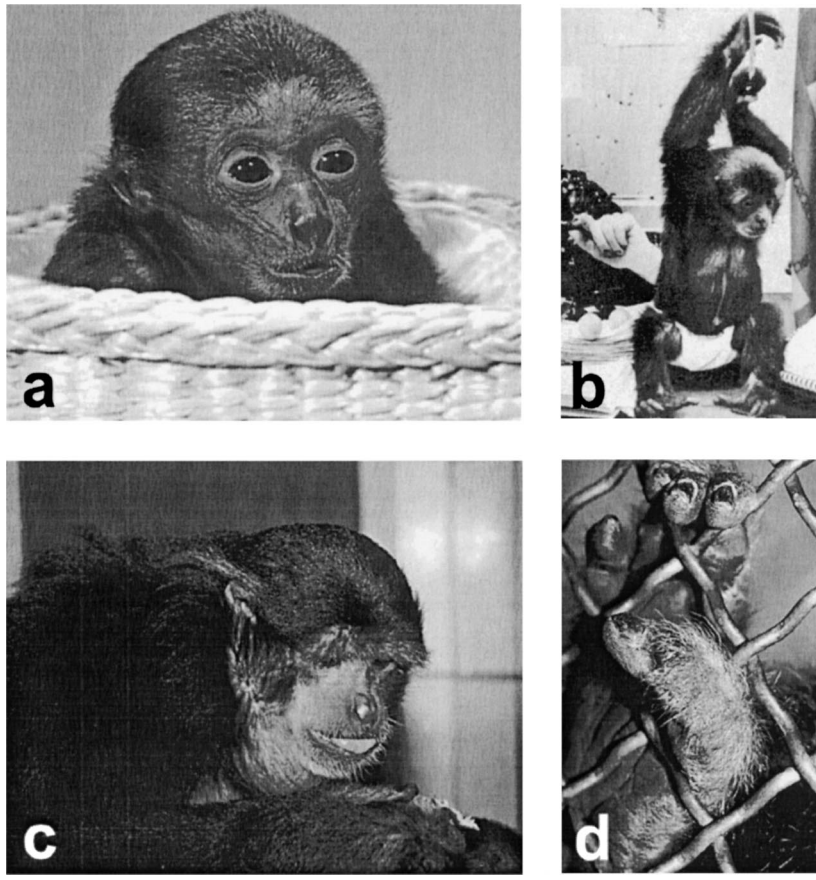

Fig. 4. Siamang female Trine at the Duisburg Zoo: (a) at the age of 11 weeks (in December 1974, photo by Dr. Hans Jesse), (b) at the age of about 8 mo (in May 1975, photo by Rolf Preuss). Notice that the facial markings and the corona were very weakly developed in the young infant (a) but soon developped into two distinct separate patches of white fur laterally above the eyes and into a broad whitish corona (b). Only later did the patches become connected to form a continuous brow band. (c) The adult female in March 1988. Notice how the corona is now reduced to a tuft of white hairs above each ear. (d.) The halluse (right foot shown) is covered with pure white fur.

9 mo old and has become very distinct since then (Mr J. Hammes, personal communication). In another male Cebulon, the pattern developed soon after birth and was much more pronounced than that in Thao, and at least as distinct as that in Trine (Fig. 5; Mr J. Hammes, personal communication).

Photographs in the archives of Duisbarg Zoo evidence the origin of the white tufts over the ears in Trine: Fig. 4b clearly demonstrates that age *ca.* 8 mo, she had a fully developed bright corona. Only when she matured was its crown reduced, but the tufts above the ears remained.

The proportion of siamang with light brow bands is similar in adult (5.6%, 9 of 162) and in immature individuals (2.3%, 2 of 88). The difference is not statistically significant (Fisher exact test, $p > 0.05$) and the result remains the same if the Duisburg lineage is included (Chi-square test, $p > 0.05$).

Among immature siamang of known sex ($n = 76$), the brow band occurred in 1 male and 1 female (or 3 males and 1 female, if the Duisburg lineage is included). In contrast to the finding on adult siamang, the brow band in immature siamangs does not appear to be more common in one sex (Fisher exact test, $p > 0.05$). If the Duisburg siamang are included ($n = 83$), the result remains the same.

DISCUSSION

I have presented the first evidence of the occurrence of a white brow band in siamang. The characteristic occurs only in 4.4% of the 250 siamang in my sample. Its frequency of occurrence is *ca*, 10 times higher (43%) in the genealogy of the Duisburg lineage which may may have been reinforced by some inbreeding (Fig. 2). Adults exhibit some sexual dimorphism in the trait: The brow band occurs significantly more often in females than in males. No sexual difference characterized a much smaller sample of immature siamangs.

The occurrence of a white brow band in siamang indicate that the genetic substrate for the formation of face markings typical of other gibbons is also present in the siamang. However, its phenotypic manifestation seems to be rare and may be genetically suppressed. If this is true, then the facial pattern in gibbons would be a primitive characteristic, and the absence of the pattern in Kloss gibbons and siamang would be a derived condition. This finding supports the opinion of Groves (1972), but contrary to studies Creel and Preuschoft (1984; Haimoff (1983; Haimoff *et al.*, 1982, 1984), who labeled the absence of a facial pattern as a primitive character state in analyses of gibbon phylogeny and systematics.

There are two other possible interpretations of the occurrence of the brow band in siamang: (1) The occurrence of the trait in the Duisburg lineage could be the result of a mutation *de novo*; its resemblance to the facial markings of other gibbons would then be pure coincidence. This interpretation appears to be less plausible because my sample contains several unrelated siamang, which also exhibited the trait, (2) The occurrence of a brow band in siamang similar to that occurring in other gibbon species could be the result of a homologous mutation. Although a plesiomorphic interpretation appears more likely, the homologous mutation hypothesis cannot be ruled out.

Further evidence is available indicating that the brow band characteristic in the Duisburg siamang is instead an atavistic trait which corresponds

to, and is homologous with, the facial patterns in other gibbons: in Trine, white hair occurs on other parts of her body. This finding is of interest, because the parts affected by the white coloration are exactly those which show diagnostic white or pale coloration in some other gibbon species: a bright or white corona is typical of pileated gibbons (*Hylobates pileatus*: Geissmann, 1994, 1995), Bornean agile gibbons (*H. agilis albibarbis*: Marshall and Sugardjito, 1986, p. 141), and—at least in certain developmental stages, but rarely in adult males—in crested gibbons (*Nomascus concolor*, *N. gabriellae*, *N. leucogenys*: Geissmann, 1989). Light hands and feet are characteristic of white-handed and pileated gibbons (*Hylobates lar* and *H. pileatus*, respectively), but also occur in some hoolock females (*Bunopithecus hoolock*, especially in *B. hoolock leuconedys*: Groves, 1972, p. 66) and in about 24% of individuals of *Hylobates muelleri funereus* (Marshall and Sugardjito, 1986, p. 143). It is important to note that in the Duisburg siamang no white marking occurs in the body parts where it would be atypical for other gibbons, for instance on the chest, arms, or legs.

The photographs in the archives of the Duisburg Zoo provide additional evidence supporting the interpretation that the white tufts over the ears in one of the siamang females correspond to a white corona: The female with the white ear tufts, at *ca.* 8 mo, had a fully developed bright corona, which was at least as conspicuous as those of species in which a corona is occurs regularly. As the individual matured, its crown was apparently reduced until only the tufts above the ears remained.

My findings suggest that white markings in siamang can be interpreted as reappearances of a primitive feature of fur coloration in ancestral siamang and other gibbons, whereas the common monochrome black fur in extant siamang represents a derived character-state in gibbons. While most authors consider white hands and feet in gibbons as a derived characteristic (Creel and Preuschoft, 1984; Groves, 1984; Haimoff, 1983; Haimoff *et al.*, 1982, 1984), I have presented evidence for the opposite view for the first time.

The full face ring may be the ancestral form of light face markings in gibbons, because adult gibbons with complete face rings occur in all hylobatid genera except *Symphalangus*, e.g., female *Bunopithecus hoolock*, female *Nomascus leucogenys*, and *Hylobates lar*. Immature *Hylobates* often exhibit more complete or broader face rings than their adult counterparts, e.g., *H. agilis*, *H. lar*, *H. pileatus*, (www.gibbons.de). Gibbons with light brow bands only, light cheeks only, or without facial markings probably represent derived character states.

Some degree of sexual dichromatism in the light facial ornaments also appears to have occurred in the common ancestor of all gibbons. It occurs in all hylobatid genera, e.g., *Bunopithecus hoolock*, *Nomascus gabriellae*, *N. leucogenys*, *Hylobates agilis*, *H. pileatus*), and *Symphalangus*.

APPENDIX

Brow-banded siamang in museum collections and zoos, with comments on the in origins and the expression of the brow band

Comments on the specimen	Brow band description
Museum specimens	
AMNH 102723, adult female, skin and skull at the American Museum of Natural History, New York, collected by J.J. Menden on 2 June 1934 at "Moeara Doewa" (=Muara Dua), Palembang, Sumatra. Original field number 121. The skull with teeth worn to basins indicates a very old animal.	Distinct whitish brow band, about 1.2 cm broad. Traces of a corona above ears (short light hairs below longer black ones). Some whitish hairs also occur on the lateral neck and on the digits, especially on big toes, but not conspicuous. Single yellowish hairs also occur in the inguinal area.
MRNH d, adult female, skull still inside skin, skin at the National Museum of Natural History, Leiden, collected by S. Müller in 1837, at Padang, Sumatra. Cat. no. 4.	Traces of a thin brow band which is thickest in its central part (glabella) and consisting of short, yellow hairs.
ZMB 38576, female, adult size, skin at the Museum für Naturkunde der Humboldt-Universität, Berlin, collected by W. Volz in Sumatra.	Yellowish brow band, relatively broad, distinct, traces also go around chin.
ZMB 38577, female, adult size, skin at the Museum für Naturkunde der Humboldt-Universität, Berlin, collected by W. Volz in Sumatra, 1904/1905.	Yellowish brow band, weak, less distinct than in ZMB 38576.
Zoo siamangs	
Hexe, adult female, wild-born about in 1960, arrived in Duisburg Zoo (Germany) about in 1964. Observed there by the author in June 1987 and March 1988.	Broad, light gray brow band, arched upwards above each eye. Broader and more whitish laterally and thinner in the middle above the nose.
Trine, adult female, born at Duisburg Zoo (Germany) in September 1974. Zoo Archive photographs made in May 1975. Observed by the author in June 1987 and March 1988. Photographs made by Ms B. Minnemann in August 2000.	Broad, light gray brow band, forming one continuous arch or chevron shape. (As an infant, the brow band consisted of two separate, light gray patches laterally above the eyes.)
Püppi II, adult female, born at Duisburg Zoo (Germany) in June 1977. Observed there by the author in June 1987 and March 1988.	Broad, light gray brow band, arched upwards above each eye. Thinning out laterally and thicker in the middle above the nose.
Thao, infant male, born at Duisburg Zoo (Germany) in January 1991. Photographs made by Dr. Mathias Orgeldinger in June 1991.	Brow band consisting of two separate, light gray patches laterally above the eyes.
Cebulon, infant male, born at Duisburg Zoo (Germany) in January 1991, died in November 1992. Photographs made by Dr. Mathias Orgeldinger in November 1992.	Brow band consisting of two separate, light gray patches laterally above the eyes.

Appendix (*Continued.*)

Comments on the specimen	Brow band description
Whoopie, adult female, born at Duisburg Zoo in April 1994, transferred to Jaderberg Zoo (Germany) about in 1998. Photographs made by Ms B. Minnemann in August 2000.	Brow band consisting of two very broad light gray tufts hanging down laterally above the eyes, which are connected by a narrow gray band.
Gaspa, adult female, wild-born about in 1963, arrived at Zürich Zoo in July 1980, observed there by the author in regular intervals 1980-1989, transferred to Thrigby Hall Zoo (U.K.) in August 1989, died in September 1990.	Pale brow band less distinct than in the adult animals from Duisburg.
Vreneli, adult female, wild-born about in 1963, arrived at the "Seeteufel" Zoo in Studen (Switzerland) about in 1967, observed there by the author repeatedly in 1981.	Pale brow band less distinct than in the adult animals from Duisburg.
Sasak, infant twin female, born at Zürich Zoo (Switzerland) in May 1992, observed there by the author repeatedly in 1992–1994 (see Dal Pra and Geissmann, 1994).	Brow band consisting of two separate, light gray patches laterally above the eyes.
Jogog, infant male, born in July 1993 at Howletts Zoo (U.K.). Photograph made by Ernie Thetford in March 1994.	Brow band consisting of two separate, light gray patches laterally above the eyes.
Kajang, adult male, wild-born about in 1964, arrived at Twycross Zoo (U.K.) in March 1971 (Badham, 1988; Badham and Richards, 1991). Observed there by the author in October 1988.	A broad whitish band arching across the forehead, slightly thinner in the middle. Whitish hairs are also interspersed in the black fur on the ventral fur of the thighs, and on both sides laterally and distally on the belly. The whitish area on the animal's forehead is separated from the facial area by a stripe of black fur which was broadest (about 2 cm) in the midsaggittal plane. As the brow area itself is black, the whitish coloration on the forehead and on other parts of the body may or may not be related to the brow band characteristic described in this paper.
Bali, adult female, wild born about in 1972, arrived at Lourosa Zoo (Portugal) in Feb. 1995. Video-recordings made by Alberto Caeiro P. de Sousa in March/April 1997.	Brow band consisting of two narrow light gray tufts hanging down laterally above the eyes, which are connected by a narrow gray band.
Unnamed adult female, wild born, observed at Ragunan Zoo, Jakarta (Indonesia) in Sept. 1998 and Jan. 2001.	Graybeige brow band, relatively broad.

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